example, which is nearly paralleled by other specimens in the National Collection.   The skull, however, is characterized by the excessive reduction of the nasal bones, which is carried to a much greater extreme than in the typical specimen of *Neotragus kirkii*, Günther (P. Z. S. 1880, p. 20).   There are also other points of difference when the skulls are compared together.

But as *Neotragus kirkii* is from nearly the same country, I think it would be hardly justifiable to name a second *Neotragus* from Somali-Land without a better series of materials to base it upon.   I will therefore content myself with calling attention to their divergencies, and, as Mr. Phillips has empowered me so to do, with depositing his specimens in the British Museum to await further inquiries.

From the discoveries made by Mr. Hagenbeck's collector, Herr Menges[1], and Messrs. James and Lort Phillips, it is quite evident that there is yet much interesting work to be done among the Mammalia in Somali-Land, and I trust that we shall soon receive additional specimens and further information concerning this interesting animal.

December 7, 1886.

Prof. Flower, LL.D., V.P.R.S., President, in the Chair.

Prof. Bell exhibited and made some remarks on a specimen of *Tænia rana*, the smallest known human parasite, which had lately been obtained for the Museum of King's College.

The following papers were read:—

1. Observations on the Development and Structure of the Ovum in the Dipnoi. By Frank E. Beddard, M.A., F.R.S.E., Prosector to the Society, and Lecturer on Biology at Guy's Hospital.

(Plates LII.–LIV.)

The present paper is the continuation of a research into the structure of the ovary in *Protopterus*, the main results of which have already appeared in the last number of the 'Proceedings.'   Besides being able to give a more complete account of the ovarian ova in *Protopterus*, I am also able to supplement this account with some few notes respecting the structures to be observed in the ovary of *Ceratodus*.   The opportunity of studying *Ceratodus* I owe to the kindness of Prof. Lankester and Prof. G. B. Howes.   The material was taken

[1] *Cf.* Sclater, P. Z. S. 1884, p. 538; Noack, Zool. Gart. xxvi. p. 172 et xxvii. p. 39; Kohl, Ann. d. k. k. naturhist. Hofmuseums, i. p. 75 (1886).

from fishes which had been preserved entire in alcohol, and was unfortunately not in a very first-rate condition for microscopical investigation.   I have been able, however, to make out the important fact that there is an essential similarity in the structure of the ovarian ova in both forms, and that in *Ceratodus,* as in *Protopterus,* there are, besides the ova, certain other structures resembling ova in many particulars which have a different mode of development.   The discovery of this fact in *Ceratodus* renders it practically impossible to suppose that the remarkable processes in the development of the germinal cells of *Protopterus,* described and figured by myself in this and my last paper, are in any way abnormal ; it had occurred to me before that there might be something abnormal.

It cost me a great deal of labour, in the way of cutting sections, to ascertain that there was an actual resemblance between *Ceratodus* and *Protopterus.*   In my specimen of *Protopterus* I found it quite impossible to make a section of the ovary anywhere without dis covering ova of both kinds in nearly equal abundance ; in *Ceratodus,* on the other hand (and this statement applies to two specimens), ova of the second kind were extremely rare ; I have cut literally hundreds of sections without coming across any evidence of the existence of two kinds of ova.   This may be a real difference between the two genera, or may depend upon the season of the year at which the specimens were captured.   In every case, however, the ovaries contained numerous mature ova, though the number of these latter was very much less than that of the immature ova.

On the other hand, it is possible that there is really a difference in this respect between *Protopterus* and *Ceratodus,* which show other important anatomical differences.

I have already contributed to the 'Zoologischer Anzeiger' (No. 236) a brief note of the principal facts contained in this paper.

I have but little to add to my former paper on the structure of the ordinary ova of *Protopterus.*

In my last paper I drew attention to the curious specialization of the yolk in the adult ova ; in fig. 4 of plate xxviii. of that paper is illustrated an adult ovum which shows a differentiation of the yolk into two distinct layers, which are less distinguishable by their coloration or arrangement of yolk-particles than by the very definite break which separates them.   The outer layer of yolk forms a com paratively thin envelope, the greater portion of the ovum being occupied by the central mass of yolk.

Van Bambeke [1] has recently noted and figured a similar condition of the ripe ovum in *Gobius niger* and other fishes, and Pflüger had previously referred to the same phenomenon in Mammalia.   Ac cording to Van Bambeke, the distinction between the two zones occasionally disappears under the influence of reagents.   Van Bam beke speaks of the line of division which separates the two zones as not being a membrane, but merely a condensation of the egg protoplasm.   With this opinion I fully agree : in the first place, the

[1] Arch. d. Biol. t. iv. (1885).

division of the ovum itself into two zones by a definite membrane would seem to be an absurdity; in the second place, no membrane was evident in preparations where the ovum was broken. It might be expected that when the ovum was broken in cutting, the membrane, being presumably of a different hardness to the egg-protoplasm, would project from the cut surface; in no instance, however, did the broken surface show any indication anywhere of a membrane. The line of division between the two yolk-zones presented the appearance in my preparations of an absolute break; the protoplasm was perfectly transparent, and, being unaffected by the staining-reagent, was invisible.

I did not notice this differentiation of the yolk in all the large ova visible in my sections. In some ova, which were full of yolk, and of equal size with those just referred to, there was no trace of any such specialization into a peripheral and central zone; in these cases the yolk was uniform throughout. Such ova were to be found not only in the same ovary, but in the same section with the ova which displayed a differentiation of the yolk. This circumstance renders it improbable that the effect of reagents has caused the yolk to acquire a uniform appearance.

A comparison of the two kinds of ova has led me to the conclusion that the ova in which there is a specialization of the yolk are nearly mature, while those in which the yolk is uniform are degenerating ova.

Another matter relates to the structure of egg-membranes and their homologies, where I have to make a correction.

In my former paper I have referred to the presence in comparatively young ova of a vertically striate membrane lying within the vitelline membrane (*loc. cit.* p. 273, pl. xxviii. fig. 1, *z.r*; pl. xxix. fig. 2, *z.r*). This, it now appears to me, is not the equivalent of the inner of the two membranes which surround the Teleostean ovum [1]. The early disappearance of this membrane and its general structure (granular and with no distinct line of separation from the subjacent egg-protoplasm) were against such an interpretation; I now identify it with more confidence with a specialized layer of the egg-protoplasm described by Brock in *Alburnus lucidus, Salmo fario*, and *Perca fluviatilis*, and by Owsiannikow in *Acerina vulgaris*. Brock has figured this layer (the "Zonoidschicht" of His, the "helle Rand-schicht" of Gegenbaur) in *Alburnus lucidus* (Morph. Jahrb. Band iv. pl. xxviii. fig. 12, *f.g.*), where it is more complicated than in *Lepidosiren* and consists of two layers—an inner homogeneous and an outer vertically striate layer.

Contents of the Ovary of Protopterus.

The following is a detailed account of the structure and development of certain bodies in the ovary which have already been partly described in my former paper; they are nearly as numerous as the ordinary ova.

[1] *Cf.* J. T. Cunningham, "On the Mode of Attachment of the Ovum of *Osmerus perlanus*," P. Z. S. 1886, pt. iii. p. 292, pl. xxx. fig. 4, *z.r.i*, and other memoirs.

Stage I.—The earliest stage of these bodies is represented in fig. 1 ; its different constituents are figured, highly magnified, in figs. 5, 14–20.

The whole structure is situated near to the surface of the ovary, with which indeed it is still in continuity ; the germinal epithelium (*ge*), which is apparently not everywhere present as an external layer in the adult ovary, is here conspicuous by its presence ; it forms a mass of cells, the nuclei of which are so large and so closely pressed together that I have found it impossible to detect any cell-outlines (see fig. 1). These thickly clustered groups of epithelial cells seem to correspond to the " epithelial islands " of many writers (see Iwakawa, G. J. M. S. 1882, p. 266). The nuclei of these cells are deeply stained by borax carmine, and for the most part rounded or oval in contour, though frequently (perhaps owing to the hardening-reagent) some- what angular. The staining-fluid is not evenly taken up by the whole nucleus, but a peripheral layer, sometimes confined to one pole of the nucleus, is very deeply stained, the central regions being compa- ratively pale.

The germinal epithelium is immediately continuous with a mass of cells which form a hollow sphere, partly occupied by a plug of cells of a somewhat different appearance ; the spherical mass of cells is quite close to the surface and connected with the germinal epithelium by a very short neck, which is as wide as the area occupied by the patch of germinal epithelium.

The peripheral mass of cells is already differentiated into two distinct layers, which are distinguishable from each other by the characters of the component cells and more particularly of their nuclei.

The outermost layer is of course the one that is in contact with the germinal epithelium ; the outlines of its cells are not very visible in my preparations : between the nuclei of the cells is a fibrous substance moderately stained by borax carmine ; this appears to me to be the slightly altered protoplasm of the germinal cells themselves, and not to be an inroad of connective-tissue stroma-cells. The germinal cells bear, however, a very striking resemblance to connective-tissue cells.

Balfour has figured (Q. J. M. S. 1878, pl. xvii. fig. 10) and described (p. 390) a condition of the Elasmobranch ovary which is so far very similar to that which I have just described, and which gives me greater confidence in stating that the cells displayed in fig. 1, *f.é*, of Plate LII. are really germinal and not stroma-cells.

He says (p. 391) :—" The surface of the ovarian region . . . is covered by a distinct . . . pseudo-epithelium . . . The cells of the pseudo-epithelium have one peculiarity very unlike that of ordinary epithelial cells. Their inner extremities are prolonged into fibrous processes which enter the subjacent tissue, and, bending nearly parallel to the surface of the ovary, assist in forming the tunic spoken of above. This peculiarity of the pseudo-epithelial cells seems to indicate that they do not essentially differ from cells which have the character of undoubted connective-tissue cells, and renders

it possible that the greater part of the tunic, which has apparently the structure of ordinary connective tissue, is in reality derived from the original germinal epithelium, a view which tallies with the fact that in some instances the cells of the tunic appear as if about to assist in forming the follicular epithelium of some of the developing ova."

The nuclei of the peripheral layer of cells are much like those of the proliferating germinal epithelium, though not quite so darkly stained—perhaps for mechanical reasons. Their shape varies considerably, some being rounded and some more fusiform; but these two extremes are united by numerous intermediate conditions. For the most part the nuclei have taken up the staining-fluid unequally; a patch at one extreme of the nucleus is more darkly coloured, and from this radiate slender threads towards the opposite extreme of the nucleus; the interstitial part of the nucleus is stained of a pale pink. The different forms of these nuclei are represented in fig. 5. The differential staining of the nucleus undoubtedly corresponds to the differentiation of its substance; and the star-like form of the darkly staining part suggests a connection with the phenomena of nuclear division; but I have not observed any cases in which the centres of the star-like bodies in two adjacent nuclei were opposed; in every instance the darkly stained extremity of the nucleus was directed away from the germinal epithelium and along the axis of the layer of cells; this uniformity in the nuclei gives them the appearance of being in rapid motion, of being as it were swept along by a current round the periphery of the sphere of cells.

Here and there the continuity of the layer of cells is interrupted by blood-vessels (*b.l*), usually of small dimensions, which are the fore-runners of the richly developed vascular supply of these same bodies in later stages of development. The appearance of blood-vessels was more common on that side furthest from the germinal layer than on that nearest to it.

Towards the opposite extremity of the sphere of cells, *i.e.* that furthest removed from the outside of the ovary, the character of the nuclei of the peripheral layer of cells becomes changed. In this region the nuclei have lost the peculiar arrangement of the nuclear substance and present the appearance of ordinary nuclei (fig. 5 *a*); that is to say, they are oval bodies with finely granular contents and here and there round, darkly stained particles which are disseminated throughout the nucleus.

Within the peripheral layer of cells is another layer of cells which becomes ultimately comparable to a follicular epithelium. Even in this early stage of development it is for the most part distinguishable from the outer layer of cells; the distinction is not only in the character of the cells and their nuclei, but in an absolute line of demarcation which separates the two layers; this consists (fig. 1, *x*) of a narrow band of structureless substance, which bears the closest possible resemblance to a substance produced by the fusion of some of the central cells of the sphere, and which will be described shortly. It is possibly formed by a metamorphosis of the peripheral layer of

the follicular cells, but serves at any rate to determine accurately the boundary line between the follicular layer proper and the mass of peripheral cells which ultimately bear a resemblance to the secondary follicle layer.   This limiting band of structureless substance is only met with on that side of the cell-mass towards the outside of the ovary ; elsewhere the cells of the follicular epithelium are perfectly continuous with the cells of the peripheral layer.

The nature of the cells of the follicular layer also differs from that of the more peripherally placed cells.   The cells themselves are rather larger and irregularly rounded in form ; there is no trace of the connective-tissue-like structure described above, in the case of the extra-follicular cells.   The cell-contents are clear and for the most part hardly affected by the staining-agent, which has coloured their nuclei deeply ; the part of the cell-protoplasm that is coloured is tinged very faintly and shows a reticulate arrangement.   The nuclei of the follicular cells differ for the most part from those of the extra-follicular layer by being rounded and even in shape, and all closely similar in size ; they are deeply stained, and show a tendency to the same reticulate arrangement of the nuclear substance that has already been mentioned in the extra-follicular cells.

The character of this follicular layer is much the same throughout, only differing in places by the more or less crowded condition of the nuclei, indicating a more or less active multiplication of the cells.   On that side of the cellular mass which is furthest from the outside of the ovary, the follicular layer comes into closer relations with the extra-follicular epithelial layer, though still recognizable. The character of the cells and of the nuclei which make up the extra-follicular coat of cells alters, and every transitional condition is met with between these cells and the cells of the follicular epithelium. This seems to indicate that the follicular layer is formed as a differentiation of the mass of invaginated germinal cells.

The whole body is thus surrounded by three distinct and independent layers—(1) the single layer of large follicular cells ; (2) a vascular layer, to which reference has already been made and which is extremely developed ; (3) an outermost cellular layer, consisting of flattened cells with nuclei elongated in the direction of the circumference of the ovum ; this layer, like the follicular layer, is only one cell thick.

For the most part this outer layer has been neglected by writers, or else has been confused with the true follicular layer.   Balfour, however, has recognized it in the Elasmobranch ovum [1] and has proposed to call it the " secondary follicle-layer.''   Owsiannikow figures this layer in the ovum of the Perch [2] ; in the explanation of the figure it is called the follicular layer, while the true follicular cells are termed the " granulosa '' ; in the text of his paper, however, the term endothelium is constantly used for this layer, which is stated to be made up of several rows of cells in many fishes. Concerning the origin of this layer Balfour expresses with hesitation

[1] Quart. Journ. Micr. Sci. vol. xviii. (1878), p. 405, pl. xix. fig. 29, fe'.
[2] Mém. Acad. Sci. St. Pétersbourg, t. xxxiii. (1885) no. 4, pl. i. fig. 4, a.

the opinion that it may be derived from the germinal epithelium. Owsiannikow suggests three possibilities [1]—either it originates from cells which have made their way out of the blood-vessels (!), or from cells of the subgerminal tissue (stroma ?), or, finally, they may be derived from the germinal layer. The latter alternative is adopted by Owsiannikow on certain evidence, which he does not, however, regard as conclusive. The outermost follicular layer of *Lepidosiren* I have already (p. 509) shown without doubt to be derived from the germinal epithelium ; I shall therefore adopt the name of *secondary follicular epithelium* for this capsule, which indicates that its origin is similar to that of the true follicular epithelium, which may be briefly termed the *follicular epithelium.*

The two layers that have just been described form a hollow sphere enclosing a central cavity, which is partly occupied by a mass of cells. It is very possible that in the fresh condition the central mass of cells occupies the whole of the space available, but this is not the case in my preparation. A large portion of the central cavity, particularly on the side turned towards the exterior of the ovary, is quite empty, and no structures intervene between the central mass of cells and the follicular layer. On the opposite side, however, the central mass is in close contact for a considerable area with the follicular cells, this area exactly corresponding with the transitional area between the follicular and external layers. These facts would suggest that the central cells are derived from the proliferation of the follicular cells and ultimately of the extra-follicular cells, as these two latter have been shown to be perfectly continuous, the proliferation taking place in a certain limited area only. In this case the apparent cavity which separates the central cells from the follicular on one side will be an indication (exaggerated by the action of the preservative reagent) that there is here no real connection between the central and peripheral layers, though they may be in actual contact in the fresh state.

A number of the central cells are displayed in figs. 14–20 of Plate LIII. ; they are more or less irregular in shape, rounded, and of different sizes ; the staining-reagent has hardly affected the cell-protoplasm, but has deeply stained the nucleus. The cell-protoplasm is arranged in a reticulate fashion, and closely resembles that of the follicular cells. Some of the cells contain two or more nuclei, which seems to show that the cells themselves are in a condition of multiplication. The most remarkable fact about the nuclei of the central plug of cells is their great inequality in size : some of the variations are exhibited in those figures ; the variation is all the more remarkable as it does not occur in the follicular layer, the nuclei of whose cells are of quite a uniform size. There is almost every gradation in size between the smallest and largest nuclei, a fact which perhaps indicates that the smaller ones are the result of nuclear division. The largest nuclei rather excel in size those of the follicular epithelium. There is a similar difference of size in the peripheral layer of cells, particularly obvious at those points where the peripheral layer is in

[1] *Loc. cit.* p. 30.

contact with the interior mass of cells, the follicular layer being at
such points indistinguishable.

It is possible that the difference of size in the nuclei corresponds
to a distinction between " primitive ova " and " germinal cells " such
as has been described by Semper, Balfour, and so many writers in
other Vertebrata ; in this case the larger nuclei will be the primitive
ova. This suggestion must be of course only regarded as such ; I
have no real evidence to offer except the different size of the nuclei.

In very many instances a degeneration of the nuclei could be
observed. This takes place in several ways, some of which may be
stages in the same series. Some of the nuclei (figs. 14, 17) remain
of the same size and shape as the normal nuclei, but show a much
paler colour and fewer nucleoli ; in one instance (fig. 15) I observed a
commencing disintegration of the nucleus, the substance of which
appeared to be in a condition of solution at one point where it passed
gradually into the substance of the cell, the limiting membrane of
the nucleus being here invisible. In other cases (figs. 19, 20) the
nuclei are as darkly stained as the normal nuclei or even rather more
so, but instead of presenting a uniform oval contour, the nucleus was
variously contorted and irregular in shape.

The centre of the mass, however, is not entirely occupied by cells
like those that have just been described. There is a certain amount
of an amorphous substance (fig. 1, p), well stained with the borax
carmine, which lies in patches between some of the central cells, and
particularly on the outside, in the space which separates them from
the follicular layer. This substance is of an homogeneous appear-
ance, though lighter in colour in some regions than in others ; it is
rather more abundantly developed in the stage next to be described
than in the present (cf. fig. 9, Plate LIII.). This substance encloses
patches of cells, or sometimes single cells ; occasionally the proto-
plasm of the cells has undergone a certain change at the periphery,
where it gradually passes into the homogeneous mass surrounding
it ; frequently scattered nuclei are to be found imbedded in it, and a
comparison of these nuclei with those of the central cells shows
them to be identical. The general appearance of the homogeneous
substance suggests a coagulated fluid, and it is very like the liquor
folliculi of the Mammalian ovum coagulated by alcohol ; but this
substance cannot be excreted by the central cells or by the follicular
cells, because it contains numerous traces of them in the shape of
free nuclei with or without a certain amount of partially altered
protoplasm attached. These facts rather indicate that the sub-
stance in question is produced by the alteration and fusion into a
semifluid mass of some of the central cells. This mode of formation
is, however, not opposed to a comparison with the Mammalian
liquor folliculi, which has been asserted by some to have a similar
origin ; the great difference is that this semifluid substance has the
power of forming yolk, as will be seen after the description of the
later stages.

There are other bodies which seem to be referable to the stage just
described, though differing in certain structural particulars as well as
in their smaller size.

These, like the last, are connected with the germinal epithelium, covering the outside of the ovary, by a pedicle of epithelial cells, which is nearly of the same width as the whole structure and its follicle. The germinal epithelium is in a condition of very active multiplication, the nuclei being very closely crowded together.

The layers of cells which surround the central mass cannot be differentiated; they present the appearance of a mass of cells continuous with the germinal epithelium and forming a layer of cells three or four deep; only here and there (fig. 10, *bl*) were traces of the irruption of the stroma in the shape of small blood-capillaries. The cells which constitute this peripheral layer are precisely similar in their character to the cells which form the outermost of the peripheral layers in Stage I.

In two instances belonging to this stage, which I have been able to study, the homogeneous darkly-staining mass produced by the solution and fusion (?) of the protoplasm of the central cells was much more in amount than in the last described stage. Fig. 11 of Plate LIII. represents the central mass of cells, which are seen to be divided up into partly or entirely isolated clumps by the formation of this homogeneous mass, which contains also free nuclei (fig. 11, *n*). In the third case the condition of the central cells, so far as this fused mass of protoplasmic material is concerned, was much the same as in Stage I.

On the whole these facts appear to indicate that the bodies belong to a somewhat earlier stage than those just described and shown in fig. 1 of Plate LII. Their small size, the undifferentiated condition of the peripheral layers, as well as the very small amount of stroma (blood-vessels) between the cells of these layers, appear to me to point to this conclusion. On the other hand, the greater amount of change in the central cells, *i. e.* the increased amount of the deeply-staining fluid substance between isolated clumps of cells, is against such a supposition, as it is evidently a further development of a process which has only just commenced in the developing structure which I have last described. This latter reason is perhaps not a very powerful argument, because it may easily be supposed that the production of the semifluid protoplasmic substance may be hastened or retarded; the same may be said with regard to the specialization of the follicular layers, only that a specialization in the instances observed by myself goes together with increase of size of the whole body. Accordingly I am inclined to believe that the bodies displayed in fig. 9 of Plate LIII. belong to a younger stage than those illustrated in fig. 1 of Plate LII.

Stage II.—The different layers composing the follicle are more differentiated, and each individual layer is now quite recognizable.

Commencing from the outside, we have the secondary follicular layer, between which and the follicular layer proper is a well differentiated vascular layer, which is easily to be made out through the whole circumference; the blood-vessels are filled with blood, and appear as round, elliptical, or elongated according to the angle of the section. The follicular layer has the appearance of being only

one cell thick, but the nuclei of its constituent cells are so crowded together that it is not easy to be certain upon this point. The outlines of the follicular cells are in many places plainly visible, and irregular processes (Plate LIII. fig. 6) project from these cells toward the interior of the mass. This may very well be owing to the shrinking of the central mass of cells, and the consequent breaking away of its connection with the peripheral epithelium. A comparison of the complete series of sections through the developing ovum (the section fig. 6 is towards the middle of the series) shows that, whether or not there is a connection between the *entire* periphery of the central cells and the follicular epithelium, there certainly is such a connection throughout a limited area lying on that side of the ovum which is nearest the external surface of the ovary, a little above (or below) the pedicle which unites the germinal epithelium with the ovum. In this region the nuclei were more abundant and crowded together than in the central cells of the mass, and were of uniform size and rounded form ; in fact they show an exact similarity to the nuclei of the follicular epithelium, which in this stage, as already mentioned, forms a distinct layer. The mass of cells which connects the follicular layer with the central cells is therefore closely similar to the follicular layer, and has the appearance of a proliferation and growth inwards of that layer. The central cells, as in the previous stage, have nuclei of varying size ; some are long and oval, and others shorter and more spherical ; the latter resemble in every particular the nuclei of the surrounding follicular layer.

A characteristic feature of this stage is the commencing formation of yolk, which is visible here and there (figs. 27–31) in the cells of the central mass, and in the form of droplets of homogeneous appearance and varying size. This formation of yolk is not confined to the central cells, but is recognizable also in the cells which make up the follicular layer.

Here and there among the central cells are homogeneous masses, evidently the same as those referred to in the description of Stage I. as a probable resultant of the breaking-down and fusion of certain of the central cells. These masses were, however, much less developed than in the earlier stage.

This stage is evidently, from the facts above narrated, in a further condition of development than that which I have termed Stage I. ; this is also shown in the gradually-advancing separation of the peripheral layers from the germinal epithelium of the ovary.

In the earlier stage the pedicle which unites the epithelial layers with the germinal epithelium on the surface of the ovary is not only very thick, but composed almost entirely of germinal epithelial cells in a state of active multiplication. The stroma of the ovary had barely penetrated into this mass of invaginated germinal cells.

In Stage II. the body is just as near to the surface of the ovary, and there is a shallow depression on the surface of the ovary corresponding in position to the centre of the pedicle of attachment, which would appear to be the remains of the invagination of the germinal epithelium. The activity of the germinal epithelium has, however,

greatly diminished; it forms only a single layer of cells, and the pedicle which connects the body with it is almost entirely composed of stroma-ingrowths, which form for the most part a very lax net-work of fibres and cells, though denser in the middle, and sur-rounding a slender cord of germinal cells, the sole remnant of the former epithelial pedicle.

In a somewhat more advanced stage there is an identical structure with that just described as regards the specialization of the peri-pheral layers and the mass of central cells; the formation of yolk has, however, gone on much faster, and the follicular cells, as well as most of the cells of the central mass, are crammed with variously sized yolk-spherules.

Here and there, especially in the periphery of the central cells, are irregularly shaped masses of yolk-spherules (fig. 24, a), among which are occasionally discernible nuclei like those of the surrounding cells. A comparison of Plate LIV. fig. 24 with Plate LIII. fig. 11 will show how very similar in size and extent these irregular patches of yolk are to the patches of amorphous deeply staining protoplasm in the earlier stage; and I cannot but think that they are these same patches of protoplasm produced by the fusion of some of the central cells which have commenced to form yolk-particles on their own account.

Other preparations, again, seem to indicate that the fusion of certain of the central cells either does not take place at all, or takes place after the formation of the yolk. I have a nearly complete series of sections through an ovum in which the yolk has already commenced to be formed; the cells of the follicular epithelium are full of yolk-particles, as are also the central cells. The latter form a compact mass of cells containing abundant yolk-particles, but without any definite patches of yolk lying between the cells, such as could be compared to the patches of protoplasm formed by a fusion of cells. In many sections, however, of this series it happened that the central mass of cells had dropped out, so that I cannot make any positive statements about the point of discussion raised. This par-ticular instance showed very plainly indeed the connection of the mass of central cells with the follicular epithelium; the area of con-nection was very limited, as has been already mentioned in other cases.

The central cells are united with the follicular epithelium by a bridge of tissue which has every appearance of being an outgrowth of the latter; the nuclei are round and pressed close together as if in a condition of active multiplication; they pass without any break into the follicular epithelium, from the cells of which they cannot, indeed, be distinguished, and gradually on the other side into the mass of central cells. The cells of the latter have the ordinary characters that have been already described. I noticed a very large number of peculiar cells, several of which are illustrated in fig. 4; similar cells are not absent in other cases, but I never have seen them so numerous as in the present case. These cells are easily to be distinguished from the germinal cells among which they lie

34*

by their smaller size, by their very deeply stained protoplasm, and by the fact that they nearly always contain a large number (3–5) of small nuclei close together. I have not yet succeeded in detecting these cells in the follicular layers, but I am nevertheless inclined to think that they are migratory leucocytes. I am at a loss, however, to account for the almost universal division of their nuclei into four or five.

The presence of leucocytes in almost all the tissues and glands of the body is so well known that I need not give any detailed references; the presence of these cells is not, however, to be confounded with the migration of follicular cells. If, however, the identification of the follicular epithelium with a layer of immigrated leucocytes be right, there can be no distinction between the two processes. The observations recorded in this paper, however, plainly show that in *Protopterus* at least there can be no possible confusion between follicular cells and lymphoid corpuscles, which is contradicted by so many other developmental facts. Unless it can be shown that lymphoid cells may arise from the direct metamorphosis of germinal epithelial cells it is quite absurd, in the present case at any rate, to allow any homology between follicular cells and immigrated white lymph-corpuscles.

Stage III.—In this stage (figured diagrammatically in fig. 3, plate xxviiii. of my former paper) the follicular epithelium is undivided from the ovum by any trace of membrane; the cells of which it is composed have dwindled down to a single layer; their diameter bears a very small proportion to that of the enclosed mass of yolk, which has enormously increased in size. The cells of the follicular epithelium are still filled with yolk-spherules presenting no differences from the yolk-spherules which make up the substance of the contained mass. Their nuclei are conspicuous and round in shape. The follicular cells appear to continue to take a share in the nutrition of the body from the fact that they are large and well developed, and that the interstices of the protoplasmic network are largely filled with yolk-spherules: occasionally (*e. g.* figs. 7, 8, *a*) the nuclei of the follicular cells showed signs of degeneration; this is probably preliminary to the evacuation of the cell-contents into the interior. Here and there the follicular cells appeared to be proliferating, the budded-off cells moving into the interior; two such instances are shown in figs. 7, 8. It is of course a difficult matter to decide how far the appearances shown in the two figures cited are due to the proliferation and migration inwards of the follicular cells; they might be explained, by reference to earlier stages, as central cells which have still remained in contact with the follicular layer, only that they occur on all sides, and it has already (p. 511) been stated that the central cells are only in contact with the peripheral for a limited area. On the other hand, a careful comparison of the example from which fig. 8 is taken with another in pretty much the same stage of development, only younger, as evinced by its smaller size, reveals the important fact that the larger contains, in any given section, a larger number of cells in its interior than the smaller. The larger was rather more

than twice the size of the smaller body selected for comparison ; the number of cells in the interior was in correspondence with their difference in size. The larger had an average of 64 cells disseminated through the yolk in any given section, the smaller 42 ; hence the proportion between the two is as 3 : 2.

I am inclined to lay all the more stress on the mathematical statement of the case, as it allows extremely wide limits for possible errors of computation.

On the hypothesis that none of the cells contained in the yolk during later stages are derived from the migration inwards of follicular cells, it is obviously necessary to assume that they are all produced by the division of the central cells, or by certain of these cells which have persisted without division. It is true that the nuclei of the central cells in the earlier stages do multiply, but it is equally certain that others degenerate and disappear ; and it seems to me that more undergo the latter than the former change ; and I find that in the stage referred to above the smaller body contains considerably fewer cells in any given transverse section than in Stage I. It would then be expected that the larger bodies would contain fewer and fewer cells in their interior. I have, however, just stated that the result of my calculations[1] in this respect has been in the direction of proving an increased number of cells in the more mature bodies. Now, assuming that I have made so large an error as $\frac{1}{3}$ of the total number of cells in the larger, the two would still contain an equal number of cells disseminated through the yolk. But on the hypothesis there ought to be a very considerably less number of cells in the larger body. It is clear therefore that this hypothesis cannot be maintained ; and as there is no ground for assuming any third origin of the cells, it seems most probable that they have been largely derived from the proliferation of the follicular layer.

Among those which I have included in this same stage are many that are probably, owing to their smaller size, younger than others which are larger. I have not, however, thought it worth while to separate these into two distinct stages, since they are both characterized by the extraordinary activity of the follicular epithelium, and by the presence of masses of yolk in the interior of the follicle, in which are imbedded numerous cells, themselves filled with yolk-spherules. As a general rule the smaller bodies belonging to this stage can be distinguished from the larger by the more crowded follicular cells ; these are smaller, placed closer together, and not confined to a single layer in the smaller, and therefore less mature, specimens ; in the larger bodies these cells have increased in size, the nuclei are not so crowded together, and the cells form but a single layer. This condition can hardly have been arrived at by the mere mechanical growth in size of the whole body, which would tend to stretch, and therefore to reduce to a single layer of cells, the follicular epithelium ; the cells themselves must either have degenerated, evacuating their contents into the interior, or must have

[1] I have also calculated the number of cells contained in the interior of two other pairs of ova belonging to this stage, and of about the same relative size.

migrated into the interior ; the principal evidence is in favour of the latter supposition.

The central mass itself is, as already stated, mainly occupied by a mass of yolk-spherules ; these are deeply stained by the colouring-reagent.   Among the mass of yolk-spherules are numerous cells which are more scattered in later stages ; many of them are in course of degeneration, as evinced by the characters of the nuclei. In my former paper I have figured (*loc. cit.* pl. xxix. figs. 9–20) a number of such cells, and need not refer to the matter again here.

In no case could I observe the faintest trace of a germinal vesicle, nor does any one of the cells found in the interior of the body show any preponderance in size, or difference of any kind from the rest. The vascular layer is highly developed in this stage, in accord with the rapid growth of the follicular cells.

Outside the vascular layer is the secondary follicle-layer, which has much dwindled in importance, and has a still closer resemblance to stroma than it had in the earlier stages.

Contents of the Ovary of Ceratodus.

The ovary of *Ceratodus*, like that of *Protopterus*, contains, besides the ordinary ova which follow a normal course of development, other remarkable structures similar to those of *Protopterus*. The normal kind of ova, which are by far the most abundant, represent a single cell, and agree in most details of structure with the ova of Amphibia and the corresponding ova in *Protopterus*. The mature ova are filled with rounded yolk-spherules approximately of equal size, and entirely unstained by prolonged immersion in borax carmine ; the periphery of the ovum is occupied by a delicate layer of egg-protoplasm in which pigment-granules are imbedded ; the egg is covered by only a single membrane, which is moderately thick with radial pores ; the follicular epithelium is a single layer of flattened cells, of which the nuclei alone are obvious in my preparations. Some ova belonging to this stage are figured by Ayers in his paper.   In rather younger ova there is a ball of protoplasm in the centre surrounding the germinal vesicle, and not yet invaded by the formation of yolk ; the germinal vesicle has a peripheral row of germinal spots as in *Protopterus*.   The formation of the yolk appears also to be on the whole very similar to the process described in *Protopterus*.   Aggregations of yolk-granules make their appearance throughout the ovum, but do not seem to be confined at first to the peripheral layers.   In the younger stages the yolk-particles are deeply stained by borax carmine, but not in the adult ova.

I have already stated in the remarks introductory to this paper that, as regards my specimens, *Ceratodus* differs from *Protopterus* in the extreme rarity of those bodies which are apparently formed by a fusion of a number of distinct cells.   So very rare are these structures that after a diligent search I only succeeded in discovering a single case which could be in all probability referred to Stage I. in the developmental history of *Protopterus* (see p. 508).   Certain other

problematical structures will be described in this portion of my paper, although they do not appear to belong to the same series as that which I shall now describe.

The body (fig. 25) is decidedly smaller than in *Protopterus*; it corresponds, however, very nearly to the stage illustrated in fig. 9 of Plate LIII., and which is fully described on p. 513, where the slight differences which it presents from other individuals belonging to Stage I. are pointed out. The correspondence is in structure as well as in size.

The body is placed at some little distance from the external surface of the ovary, but is connected with the germinal epithelium of the surface of the ovary by a slender pedicle of cells; it consists, like the corresponding structure of *Protopterus*, of a hollow sphere of cells which enclose a central mass; the peripheral and central cells are also more or less independent. The peripheral layer of cells forms a continuous whole, but a closer examination shows it to be made up of two layers which are occasionally very distinctly separable from each other. The outermost layer appears to have originated from the germinal epithelium; its nuclei are large, rounded, or oval, and closely pressed together; the cells themselves, which contain these nuclei, have for the most part a stroma-like appearance (see p. 508). Within this layer, which is often several cells thick, is a layer of blood-vessels ensheathed in a mass of tissue of a fibrous retiform character, the fibres (fig. 25, *a*) for the most part forming a layer running parallel with the circumference of the ovum, with interspersed nuclei; this tissue, from its general appearance and from its intimate connection with the blood-cavities (fig. 25, *bl*), is probably derived, like the blood-vessels, from ingrowths of stroma. The nuclei of this presumed stroma-layer are on the whole more elongated in form than those of the outer layer; the blood-vessels were gorged with blood.

The central mass of cells is probably during life in contact with the peripheral layers, but it appeared to be for the greater part at least quite distinct from it, there being no transition between its cells and those of the peripheral layers. The central cells appear to be closely similar in structure to the corresponding cells in *Protopterus*; the protoplasm of the cell is reticulate with large spaces left between the individual strands which form the network; the nucleus is of moderate size, round or oval in shape. Here and there (figs. 25, 26, *f.e*) some of the central cells were disposed in a row, one cell thick, round the periphery, closely applied to the innermost (stroma) layer of the peripheral layers. This is possibly to be compared to the true follicle-layer in *Protopterus*.

Although, as I have already stated, the material at my disposal in the case of *Ceratodus* was not well preserved, certain portions of the ovary were in a better condition than others, and, generally speaking, it was quite possible to make out the relations of the different parts of the organ, both the stroma and contained ova, as well as occasionally the germinal epithelium on the outside; the minutiæ of structure of the different cells were disguised by the inferior

state of preservation, but in most cases the nuclei were very well preserved indeed, showing the rounded or oval form and the granular contents. This will not apply to the germinal vesicle of the ova, which were usually rather altered, showing, however, the peripheral layer of germinal spots. It does not seem likely, therefore, that the structure just described has been so altered as to render its identification impossible.

As already said, the evidence of the existence in *Ceratodus* of the structure formed by a fusion of cells depends upon only one case, which is an early stage corresponding to that of *Protopterus* figured on Plate LIII. fig. 9. This is the only example that I have succeeded in finding after a careful examination of many hundred sections. Besides these, my sections of the ovary contain a few peculiar structures, displayed in figs. 3, 21–23, which are certainly not referable to the same series as the last, and concerning the nature and homologies of which I am in great doubt. The material at my disposal was not sufficiently well preserved to enable me to speak with certainty as to every detail of structure; and I only succeeded in finding a very few of the bodies in question, so that the following account is necessarily meagre.

In fig. 3 of Plate LII. is represented what I believe to be the earliest stage: it consists of a spherical mass of cells bounded externally by an apparently structureless membrane, which separates them from the surrounding ovarian stroma (*a*); the cells are mainly disposed round the periphery of the sphere, the centre of which is largely occupied by spaces in which there is no trace of any fluid; the cells are small and rounded, with a large spherical or oval nucleus; the nucleus, but not the cell-protoplasm, is deeply stained by the reagent used (borax carmine). The cells are exactly similar to the germinal cells so far as I could see; and the conditions I shall describe in the next stage lead me to infer that they are derived from the germinal epithelium.

The second stage differs from that just described in being still continuous with the germinal epithelium; this fact would seem to point to its being an earlier stage than that just described, were it not for another difference in its structure. The body consists, like the last stage, of a mass of cells, but in the interior is a patch of granular substance, which shows a different reaction to the staining-fluid. It is hardly at all affected by the borax carmine and has a yellowish tinge. This central mass encloses here and there a few of the more peripherally-placed cells.

Of the next two stages, displayed in figs. 21–23, I am uncertain which ought to be regarded as the earlier.

In both the mass of cells has dwindled down to a single layer of peripherally-placed cells (*b*), which, as before, are separated from the stroma of the ovary by a conspicuous and apparently structureless membrane. In the centre of the cells is a spherical or oval mass of a substance somewhat granular in appearance, which is not separated from the peripheral layer of cells by any membrane, but only by shrinkage. This mass (figs. 21 and 22) is of a yellowish tint, hardly

affected by the borax carmine, and is throughout of a similar structure; there is no structure resembling a nucleus to be seen. This central mass is clearly a further development of the condition described in the second stage.

In one example, displayed in fig. 23, there is a difference from the condition just described in the presence of a few cells imbedded in the central mass, but clearly distinguishable from it by the nuclei being deeply stained. The cell-protoplasm was, however, hardly distinguishable from the surrounding mass. In the other example (fig. 21) the central mass contained no such cells.

With the exception that it possesses no nucleus, this structure resembles very closely Platner's figure of the Gasteropod ovum [1], which contains a number of cells ("Nährzellen") within its substance, derived from similar cells lying around the ovum.

The first two stages described are about equal in size; the latter two are also about equal to each other, but considerably larger (twice the size) of the former. The comparison of sizes quite supports my identification of the latter two as the later stages in development; and there can be no doubt, I think, that they all belong to the same series.

These structures obviously bear a certain resemblance to the multicellular bodies in this fish and in *Protopterus*; and if I had not succeeded in finding in *Ceratodus* another structure undoubtedly corresponding to the multicellular body of *Protopterus*, I should have certainly regarded the structures at present under discussion as the representatives of the latter.

The principal difference appears to be the non-formation of any secondary follicle-layer, the absence of any special vascular supply, and the fact that yolk is not formed in the early stages. With regard, however, to the apparent absence of the extra-follicular layer, it must be remembered that the close resemblance of the layer to a layer of stroma-cells has already been dwelt upon (p. 508). It seems to me very possible that the structure just described is formed by the fusion of the protoplasm of the centrally-placed cells, the nuclei themselves gradually disappearing.

An examination of better material must, however, settle the question.

General Conclusions, and Comparison of Ova with those of other Vertebrates and Invertebrates.

The general conclusions to be drawn from the facts, in so far as they refer to the Dipnoi, have been partly summed up in the *résumé* at the end of my former paper on this subject. It may be taken as a proved fact that the ovary in the Dipnoi contains two kinds of structures developed from the germinal epithelium. The first kind is an ovum, the equivalent of a single cell, and is similar in all essentials to the ovum in the Amphibia. The second structure, which is very commonly met with in *Protopterus* and but rarely in

[1] " Zur Bildung d. Geschlechtsproducten bei den Pulmonaten," Arch. f. mikr. Anat. Bd. xxvi. (1886) p. 599.

Ceratodus, is the resultant of a large number of cells the protoplasm of some of which undergoes certain changes and forms a more or less fluid mass with the original nuclei suspended in it; this mass appears around and between the rest of the cells, which are destined for its nutrition. The whole structure is surrounded by a definite follicular layer, which also shares in its nutrition by the formation of yolk in its cells and their proliferation inwards. These bodies are surrounded by cellular layers which correspond exactly to the layers which surround the ova of other vertebrates; the difference is that instead of there being a single cell which grows at the expense of the rest, the interior of the mass is formed by numerous cells, all equivalent.

The bodies may be distinguished as *multicellular* or *plasmodial* from the ordinary *unicellular* ova. The share which the follicular epithelium takes in the nutrition of the ovum, I have discussed in detail in my former paper and need not refer to it again here, except to remark that the elaboration of food-material in the follicular layer and its absorption by the ovum has of course no relation whatever to my view that the ovum is a cell-complex. Certain writers have adduced arguments of this kind as a disproof of the unicellular nature of the ovum, which to my mind have no force.

On the other hand, the developmental facts with respect to the cells within the follicle appear to me to be difficult to interpret otherwise than on the assumption that the ovum has the value of more than a single cell.

It is true that I have been unable to detect any earlier stages than the one figured on Plate LII. fig. 1; but the intermediate stages between that and the mature ovum are fairly complete. The discovery of the earlier stages is of great importance; it would decide among others the very important question whether the central mass of cells is, or is not, derived from primitive ova recognizable as such in the germinal epithelium, and whether or not the central mass of cells is formed by the migration inwards of a number of these cells or by the repeated division of one. But, whatever may be the answer to these questions, I have, I think, proved that the ovum is formed out of this central mass of cells. Some of these cells are apparently used as pabulum, but others fuse together into a mass of semifluid substance, which bears a very close resemblance to the liquor folliculi of the mammalian follicle. The resemblance is still more striking if we accept Waldeyer's statements that the liquor folliculi is produced by a direct metamorphosis of the follicular cells, their nuclei remaining, as in the case of *Protopterus,* suspended in it. This substance, however, in *Protopterus* has not a mere passive function, serving, as in the mammal, to aid in the expulsion of the ripe ovum, possibly also in its nutrition; it retains the activity of the cells from which it is derived and secretes yolk; it must therefore be looked upon rather as a plasmodium of these cells than a product of their degeneration, although its deep staining with borax carmine, as opposed to the very light staining of the remaining cells, indicates some chemical change. Furthermore, there is no evidence of any

one of the cells, which compose the central mass of the follicle, acquiring a predominance in size over its neighbours or being differentiated in any other way.

The fact of there being two kinds of ova with a different mode of development is not new to the Vertebrata. In my former paper I have compared the follicle and its contents in *Protopterus* to the "egg-nest" of Elasmobranchs, the points of difference being perhaps on the whole greater than the points of resemblance. But, since the formation of "egg-nests" is so general among the Vertebrata, it seems to me that there is probably some genetic connection between these structures and the "egg-nest" of *Protopterus*. It has been shown that in Mammals, Elasmobranchs, and Reptiles the permanent ova are formed in two ways:—either (1) by the direct development of one of the primitive ova, which surrounds itself with a follicular layer derived from the ordinary undifferentiated germinal cells; (2) a number of primitive ova coalesce together to form a nest; their nuclei multiply, and some atrophy, serving as pabulum for a limited number which subsequently separate off, accompanied by some of the undifferentiated germinal cells, to form as many ova. These two modes of development are not regarded by Balfour as morphologically very different; the latter mode of development has been brought about to secure the adequate nourishment of a certain number of cells which form the permanent ova.

Balfour's [1] observations certainly do not show any morphological difference between the ova produced in these two different ways; in both cases the ovum is the equivalent of a single cell; but the physiological difference is considerable.

I have referred above (p. 512) to the presence of two kinds of cells among the central cells, distinguishable by the characters of their nuclei; in some the nucleus was rather larger and more oval in form than in others, where it was smaller and rounder, and, in fact, exactly like the nucleus of a follicular cell. It is possible that the cells with larger nuclei correspond to primitive ova and the smaller to the ordinary germinal cells; in this case the resemblance of the central mass of cells to the egg-nest of the Elasmobranch will be diminished; against this supposition is the fact that there are nuclei of intermediate size, but these may have been produced by a recent division of some of the other nuclei.

Judging from analogy, however, it is probable that some of the cells of the germinal epithelium are specialized into primitive ova from undifferentiated germinal cells, although in patches of germinal epithelium covering the ovary I failed to detect any such specialization in the nuclei.

The important facts to be borne in mind in comparing the egg-nest of the Elasmobranch with that of the Dipnoi [2] appear to me to be the early formation of the complicated follicular layers in the latter and the early commencement of yolk-secretion. The germinal cells being

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[1] Balfour, *loc. cit.*

[2] It is important to remember that the formation of "nests" is not confined in Elasmobranchs to the embryonic period (see Balfour, *loc. cit.* p. 415).

filled with yolk-particles at the expense of their protoplasm must tend to lose their activity for movement, their energy being spent in the elaboration of yolk ; again, the thick layer of cells surrounding the central cells would prevent any of the central cells from leaving the interior of the follicle ; the result of further growth would therefore necessarily lead either to the development of a number of distinct ova remaining permanently within the follicle, or to the excessive development of one of the cells, which would ultimately form the ovum, or, finally, to the formation of a single ovum out of the whole mass of cells. There are no facts which point to the truth of either of the first two alternatives, while all the facts at my disposal appear to prove the third alternative ; accordingly the temporary fusion of the primitive ova in the Elasmobranch nest and the degeneration of some of them becomes permanent in the Dipnoi, the ovum being the equivalent of a whole "nest." Both Palæontology and Anatomy point to the great age of the Dipnoi, which may therefore easily be supposed to have retained ancient characters in the structure of the ova, as they undoubtedly have in the structure of the genital ducts. It is more generally believed that the Elasmobranchs are at a still lower level of organization ; if, however, as Mr. Howes has pointed out to me, the Chimæroids are the ancestors both of Elasmobranchs and Dipnoi, it may as easily be supposed that the egg-nest of the former has been derived from the egg-nest of the Dipnoi, as that the converse process has taken place. In this case the temporary fusion of primitive ova in the Sharks and Rays is a reminiscence of their permanent fusion in *Protopterus* and *Ceratodus*. It does not seem to me possible at present to say which of these views is correct ; nor indeed can any comparison at all of the two structures have any great weight until the structure of the ovary has been thoroughly examined in such types as *Chimæra* and some of the more primitive Sharks.

On the whole it appears to me possible to regard these remarkable structures in the Dipnoi as corresponding to the egg-nests of other Vertebrates ; but the apparent absence of any protoplasm in the yolk-mass renders it extremely unlikely that the structure develops into an embryo[1]; on the other hand it is often very difficult, in an ovum full of yolk, to distinguish the protoplasmic matrix ; it is probable, however, that these structures do not undergo any further

[1] I observed several ova undergoing degeneration—in one case belonging to the type discussed here. The follicular epithelium was in a condition of active degeneration, the cells becoming detached and passing into the interior of the ovum. (This process is not to be confounded with the *nutrition* of the ovum by the follicular cells recorded in this paper and in my last; in the latter case the follicular cells are large, crammed with yolk-particles, and remain a continuous layer; in the degenerating ovum the follicular cells have decreased in size, contain little yolk, and great gaps are left by the disappearance of the cells.) The yolk has also undergone great changes, the yolk-spherules exhibit a vacuolated appearance and are of more irregular size, as if a number had become converted into fat-drops and had run together; the amount of yolk also was less, and the ovum in consequence was collapsed and of irregular shape ; at several points the walls of the ovum were altogether indistinguishable. The way in which the ovum degenerates does not in fact

changes, though the degeneration of a few out of an immense number (see footnote) is hardly proof of this. If I were in a position to deny the presence of a germinal vesicle, the absence of this essential element in the ovum would be evidence of some force in the same direction. On the other hand, the energy showed by the central cells and the cells of the follicular epithelium would be entirely thrown away in this case; and it is very difficult to imagine the continuance of such a wasteful process in the ovary—the organ chiefly concerned with the preservation of the race[1].

A formation of ova in the Vertebrata by a fusion of cells has been stated to exist, but has been subsequently denied.

Goette's observations on the formation of the ovum in *Bombi-nator*[2], referred to in my former paper, have been explained away by Nussbaum[3], who considers that the polynuclear condition described by Goette is the result of the proliferation of the nucleus of a primitive germinal cell, and is not produced by the approximation of the nuclei of a number of distinct cells which subsequently are fused.

The observations of v. Siebold[4] are of interest in relation to this question.

In *Apus* the ova are formed in spherical acini which contain a number of cells of which one grows at the expense of the rest. This cell finally comes to occupy the whole of the interior of its acinus, the remaining cells dwindling indefinitely; the nucleus disappears, and yolk-formation sets in. When the cell has been, for the most part, converted into yolk it moves down the duct which connects the acinus with one of the branching tubes of the ovary, and there fuses with one or more cells which have been produced in other acini by a similar course of development. The fused mass becomes surrounded by a membrane, and is the ovum. In my preliminary notice in the 'Zoologischer Anzeiger' I have referred to the observations of v. Siebold, and

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differ very widely from a description (Arch. für mikr. Anat. 1886) of the degenerating ovum of the trout.

I may also take this opportunity of referring to an ovum of *Ceratodus* in a similar condition of degeneration. I erroneously mentioned this ovum (Zool. Anzeig. No. 236) as a nearly fully mature ovum belonging to the multicellular or plasmodial type; it may very likely belong to this type, but the appearances which it presents are indicative of degeneration, and not of maturation. The follicular epithelium is not separated by any membrane from the contents of the ovum (fig. 2); its cells in a few cases are loaded with brown pigment, and many of them have migrated into the ovum, the contents of which have been largely absorbed, probably by these cells; in consequence of this the ovum is collapsed.

I have noticed a similar state of affairs in the ovary of a newt (*Molge waltlii*), which I purpose to describe on some future occasion.

[1] It has been suggested to me, in conversation, by Prof. Lankester that these structures may serve as food for the embryos, being deposited along with the ova, or that they may be reservoirs of nutritive material aiding in the growth of the intra-ovarian ova. Either of these suggestions appears to me to be extremely plausible.

[2] Arch. f. mikr. Anat. Bd. xviii.

[3] Entwickelungsgeschichte der Unke.

[4] Beiträge zur Parthenogenese der Arthropoden. Leipsic, 1871.

erroneously stated that there had been no confirmation or refutation
of the truth of his discoveries ; I find, however, that I have un-
wittingly ignored the contents of a paper by H. Ludwig[1], in which
there are described a series of important investigations of the ovary
of *Apus*.   Ludwig finds that there is nothing abnormal in the
formation of the ova, and that a number of them do not coalesce as
stated by v. Siebold ; at least there is no real fusion of the ova, only
an accidental running together of the contents of several acini due
to ruptures.   Ludwig's account is so circumstantial, that there can
be no reasonable doubt that the ova of *Apus* are not formed by the
concrescence of several cells.   The only other instance that I am
acquainted with in which the ovum has been stated to arise from
the fusion of a number of cells is in the Rotifer *Lacinularia*.

A curiously similar mode of development of the ovum has been
recorded by Huxley in *Lacinularia*.   A number of cells of the
ovary become compacted together, enclosed in a common mem-
brane, and break away to form an ovum, which is, according to
Huxley , *never fertilized but develops parthenogenetically*.   It is
true that the statement about the non-fertilization of these ova has
been questioned by a later observer[2], but much weight must obvi-
ously be given to the observations of the discoverer of the formation
of the ' winter ova ' in *Lacinularia*.   The mode of origin of these
ova is closely parallel to that which I have described above in
Protopterus and *Ceratodus*.   The ovary in the Rotifer consists of a
mass of cells, some of which develop into ova, and all of which are
comparable of course to the germinal cells in the ovary of the
Vertebrate.   The fusion of a number of these to form a single ovum
is therefore clearly analogous to the fusion of a number of germinal
cells in *Protopterus* and *Ceratodus*.

EXPLANATION OF THE PLATES.

PLATE LII.

Fig. 1. Multicellular body in ovary of *Protopterus*, Stage I. *g.e*, germinal
   epithelium on surface of ovary ; *f.e*, follicular epithelium; *f.e'*, se-
   condary follicle-layer ; *bl*, blood-vessels ; *c*, central cells ; *n*, nuclei
   of central cells ; *p*, mass formed by the fusion of the cell-protoplasm
   of central cells.
   2. A portion of an adult ovum of *Ceratodus* in which the egg-membranes
   have disappeared prior to degeneration of ovum. *a*, stroma-layer ;
   f.e, follicular layer ; *y*, yolk-spherules.
   3. Nest of germinal cells in ovary of *Ceratodus*. *a*, nucleus of stroma-
   cell ; *b*, follicular layer ; *d*, central cells.
   4. Lymph-cells (?) from multicellular body of *Protopterus*.
   5. Nuclei of germinal cells from secondary follicle-layer of body, illus-
   trated in fig. 1. *a*, a nucleus from one of the same cells on the side
   of the body opposite to the area of invagination.

PLATE LIII.

Fig. 6. Transverse section through a portion of outer surface of multicellular
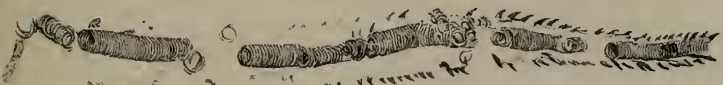
[1] Arbeit. a. d. Zool.-zoot. Inst. Würzburg, Bd. i.
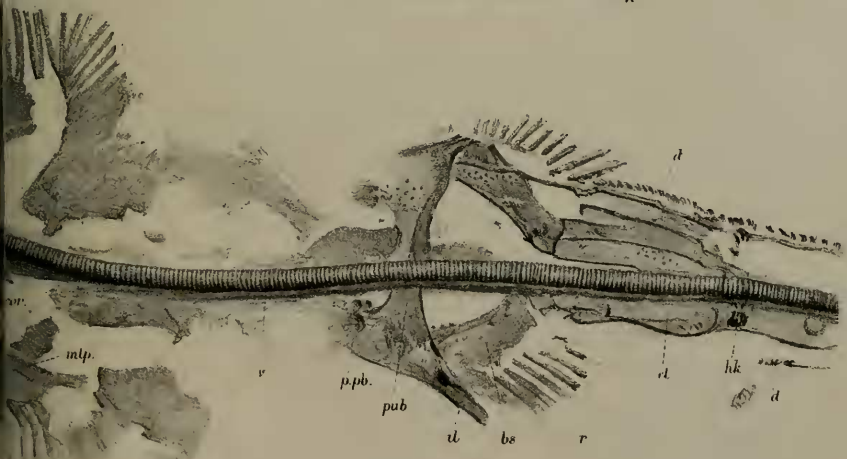[2] See Cohn, Zeitschr. f. wiss. Zool. Bd. vii. (1856).
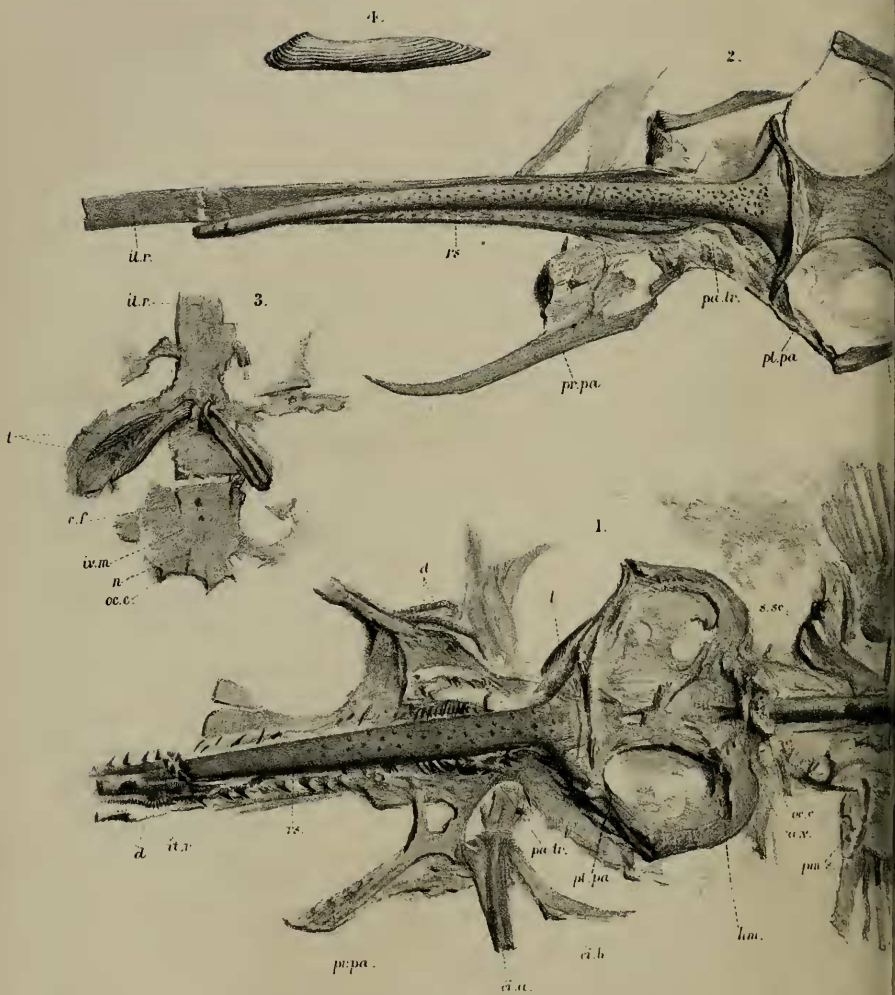
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body (Plate LII. fig. 1) in a later stage. Lettering as in last plate.

Fig. 7, 8. Transverse sections through a portion of outer surface of multicellular body in a later stage. *a*, degenerating nuclei; other lettering as before.

9. Multicellular body from ovum of *Protopterus*, differing from that illustrated in fig. 1 mainly by the absence of follicular layer. Lettering as before.

10. Portion of secondary follicular layer at point marked with an arrow in preceding figure; more highly magnified.

11. Central mass of a body belonging to same stage as that figured in fig. 9, to show the mass (*p*) formed by the breaking down of the central cells (*c*), the nuclei of which (*n*) are here and there imbedded in it.

12. One of central cells (Plate LII. fig. 1, *c*) with a large number of nuclei.

13. Three central cells from Stage I. (fig. 1, *b*), to show difference in nuclei.

14–20. Central cells very much enlarged from Plate LII. fig. 1, to show the different stages in degeneration of nuclei.

21. Nest of germinal cells in ovary of *Ceratodus* at a later stage than that in Plate LII. fig. 3. Lettering as in that figure.

Plate LIV.

Fig. 22. A portion of body represented in Plate LIII. fig. 21, more highly magnified. Lettering as in fig. 21.

23. Nest of germinal cells in ovary of *Ceratodus* at a stage near to that represented in figs. 21 and 22. Lettering as in those figures.

24. Portion of multicellular body in ovary of *Protopterus*, to show masses of yolk (*a*), apparently corresponding to areas occupied by fused masses of protoplasm in earlier stages (*p* in figs. 1, 9, and 11).

25. Multicellular body of *Ceratodus* at a stage corresponding to that of *Protopterus*, illustrated in fig. 1. *a*, fibrous tissue of stroma-layer; other lettering as in fig. 1.

26. A portion of central cells of multicellular body of *Ceratodus*, more highly magnified. Lettering as in fig. 1.

27–31. Central cells of multicellular body of *Protopterus* at an early stage, to show commencing yolk.

32, 33. Central cells of ditto, to show disintegrating nucleus.

2. On the Anatomy and Systematic Position of the Liassic Selachian, *Squaloraja polyspondyla,* Agassiz. By A. Smith Woodward, F.G.S., of the British Museum (Natural History).

(Plate LV.)

Summary of Previous Researches.

The prolific fish-beds of the Liassic formation have yielded so much valuable material during recent years, that it is now possible to considerably supplement the original anatomical memoirs of Agassiz, Egerton, and the other pioneers in early Mesozoic ichthyology. Many specific types that were at first only known from very

imperfect fragments are already represented by remains as complete as can be expected in a fossil state ; and such remains being now forthcoming in the case of the remarkable Selachian, *Squaloraja polyspondyla*, it is proposed once more to bring this interesting form before the notice of zoologists.

The first scientific account of the genus and species under consideration was communicated by Dr. H. Riley to the Geological Society in 1833, and subsequently published, with one slight modification, in that Society's 'Transactions'[1]. A fine specimen in the Bristol Museum, displaying the head and vertebral column, with obscure fragments of the appendicular skeleton, formed the subject of this memoir, and notwithstanding the author's limited means of comparison, he rightly recognized its affinities both with the true Sharks and the Rays, and expressed the circumstance in its generic name. Riley, however, misinterpreted the snout and rostral spine, regarding these as jaws, and originally suggesting the specific name of *dolichognatha* in allusion to their elongated shape ; but Agassiz pointed out to him the error in correction in an appended note (*l. c.* p. 85), and the distinguished author of the ' Poissons Fossiles' again figured and described the specimen in one of the later parts of his third volume[2]. Agassiz, indeed, was already acquainted with portions of the vertebral column and dermal tubercles of the fish, and had enumerated these in his preliminary manuscript notes under the name of *Spinacorhinus polyspondylus* ; but Riley's prior description necessitated the adoption of the generic title *Squaloraja*, though his withdrawal of ' *dolichognatha*' allowed the Agassizian specific name to be retained.

But although Agassiz's extensive acquaintance with the Selachian order enabled him to throw further light upon the Liassic genus, and point out its remarkable resemblances to the Pristiophoridæ, he still failed to comprehend the precise nature of the curious snout, and it was left to Mr. William Davies, of the British Museum, with still more materials at his disposal, to offer a complete explanation. In an important paper in the 'Geological Magazine' for April 1872[3], he pointed out that the uppermost rostral prolongation was a true spine, homologous with the frontal spine of the male Chimæroid *Ischyodus orthorhinus*, then made known by Sir Philip Egerton ; and he further demonstrated the absence of the appendage in some individuals, which were naturally regarded as females. Davies, moreover, added some notes on the vertebral column, and Hasse has more recently[4] published an account of the structure of the vertebræ in great detail.

[1] H. Riley, "On the Squaloraja," Trans. Geol. Soc. [2] vol. v. 1833, pp. 83–88, pl. iv.

[2] L. Agassiz, 'Recherches sur les Poissons Fossiles,' vol. iii. p. 379, pls. 42, 43.

[3] W. Davies, "On the Rostral Prolongations of *Squaloraja polyspondyla*, Ag.," Geol. Mag. vol. ix. (1872) pp. 145–150, pl. iv.

[4] O. Hasse, " Einige seltene paläontologische Funde," Palæontographica, vol. xxxi. (1885) p. 4, pl. i. figs. 2, 3.

New Specimens.

Up to the present time, therefore, there is no very precise information in regard to the structural features of *Squaloraja* beyond the descriptions of dermal appendages, the snout, and the vertebral column. But the British Museum again furnishes materials for an addition to our knowledge (thanks, especially, to a recent purchase from Mrs. Dollin of Lyme Regis, and the acquisition of the Egerton and Enniskillen collections), and it is upon the national fossils that the present contribution is based. All the specimens are from the well-known Lower Lias of Lyme Regis, Dorsetshire ; and, adding Roman numerals for convenience of future reference, they may be briefly enumerated as follows :—

I. The nearly complete skeleton of a male, wanting only a small portion of the caudal region, and shown of the natural size in Plate LV. fig. 1. This specimen exhibits the dorsal aspect, and is particularly interesting on account of the preservation of the limbs and limb-girdles, which have not hitherto been so well displayed. The cranial cartilages are not remarkably distinct, and the dentition is only feebly indicated ; but the form and proportions of the snout and rostral spine are very satisfactorily shown, and the vertebral column, except anteriorly, is in a comparatively good state of preservation. (Brit. Mus. no. p 2276.)

II. Portions of the vertebral column and the crushed cranium of an old individual, probably female. (Egerton Collection, Brit. Mus. no. p 2079.)

III. Portion of the skeleton of a young female, viewed from the ventral aspect. There are only obscure remains of the cranial cartilages, but the snout and dentition are beautifully exhibited. The caudal region is also well preserved, but all traces of the abdomen have been removed and destroyed. (Enniskillen Collection, Brit. Mus. no. p 3184.)

IV. A fine skull of a male individual, seen from above, and exhibiting the form of the head, dentition, and rostral spine. (Brit. Mus. no. 47402.)

V. A detached rostral spine, somewhat smaller and less robust than that figured by Davies (*l. c.* fig. 3), but equally curved, the broadened base of insertion wanting. (Enniskillen Collection, Brit. Mus. no. p 3186.)

VI. A complete, much-curved rostral spine, exhibiting only the superior aspect. (Enniskillen Collection, Brit. Mus. no. p 3187.)

VII. The anterior two thirds of a rostral spine, probably belonging to an animal even larger than no. II. (Enniskillen Collection, Brit. Mus. no. p 4574.)

VIII. An extraordinarily slender and acuminate small rostral spine, seen from the dorsal aspect. (Egerton Collection, Brit. Mus. no. p 2081.)

The specimens numbered I. to IV. are almost certainly referable to the already named species, *S. polyspondyla,* Ag., and owe their slight variability to differences in age, as indicated by the condition

of the vertebral column.   But the detached spines would appear to
afford evidence of two or more forms as yet unrecognized, and the
small example, no. VIII., is particularly distinct.   It is very possible,
indeed, that when more specimens of the genus are available for
study, the characters of the rostral appendage will enter promi-
nently into the diagnosis of each species ; but I only venture, on
present evidence, to distinguish the possessor of the small spine no.
VIII. (Plate LV. fig. 6), and this may be appropriately designated
by the name of *S. tenuispina*.   The fossil in question is separated
from its homologue in the known species by its much more slender
and acuminate shape, and possibly, though not certainly, by the
slight concavity of the proximal half of its upper surface.

During the investigation of these fossils I have had the privilege
of discussing the subject with several zoological and palæontological
friends, to whom I am indebted for some valuable suggestions noted
in the following pages.   I desire especially to return thanks to Prof.
W. K. Parker, F.R.S., for much kind assistance in regard to the
skull ; to Mr. G. B. Howes, for a continuance of the help so freely
given on previous occasions ; to Mr. G. A. Boulenger, for the facili-
ties afforded in the study of the recent Selachians under his care ;
and to my senior colleague, Mr. William Davies, to whose earlier
work reference is so frequently made in the sequel.

Anatomical Description.

External Form.—Commencing the description with a brief notice
of the general external form of *Squaloraja*, attention may be first
directed to the beautiful specimen no. I., represented in Plate LV.
fig. 1.   As the shape of the head had already led Agassiz and Davies
to suspect, the proportions are found to be very similar to those of
the living *Pristiophorus*.   Assuming that about three centimetres
are missing from the tail of the specimen, the snout will have
occupied one quarter of the entire length of the animal.   The body
must have been but slightly compressed from above downwards, and
the pectoral fins were undoubtedly free, having no connection with
the head ; the shoulder-girdle, however, is placed relatively nearer
to the chondrocranium than is the case either in *Pristiophorus* or
Pristis, though appearances are not improbably deceptive, owing to
crushing during fossilization.   It is impossible, of course, to deter-
mine whether the gill-openings were ventral or lateral, and scarcely
any traces of the branchial arches have been preserved.   The
pectoral fins, as usual, are much larger than the ventrals, and the
tail is long and slender, without spine, as admirably shown in no. III.
(fig. 7).   Unfortunately, all sure indications of dorsal and caudal
fins are wanting, though it is scarcely likely that these appendages
were absent in the living fish.

Dermal Structures[1].—In regard to the integument and its appen-
dages, the new fossils afford some interesting additional information.
No less than eight rostral spines are now available for study ; and

[1] The dentition will be more conveniently treated in a later section, p. 534.

the specimens numbered I. and III. reveal a few hitherto unnoted facts concerning the arrangement of the small prickly tubercles.

As already indicated in Davies's large figure, but still more satis factorily shown in our Plate LV. fig. 1, a series of the tubercles with especially long recurved hooklets is arranged along either edge of the prenasal (intertrabecular) cartilage ; and these two rows are precisely parallelled in the snout of certain living species of *Rhino- batus* (e. g. *R. granulatus*). But immediately at the base of the rostrum, where the cartilage is particularly firm and expanded into two lateral elevations (Davies, fig. 2), the tubercles become densely clustered in a manner not observable in the existing form ; and this arrangement is in intimate relation with the overlying spine. The disposition of the tubercles along the trunk, even if originally regular, is now no longer evident, and none but scattered examples are to be seen ; but the slender tail was provided on each side with a longi- tudinal row of comparatively large recurved hooklets, upon inconspi- cuous bases, as is very well shown in the female, no. III. (fig. 7). A small tuft of these dermal structures also occurs at the extremity of each clasper in no. I. (fig. 1, *hk*), and there are distinct indications of a patch of very minute prickles upon the membranous portion of the (right) ventral fin in the same specimen.

In regard to the rostral spine, Davies's figures and descriptions leave little to be added. The conclusion as to its absence in certain individuals (females) is confirmed in an interesting manner by the fossil no. III., which has been so " developed " on the dorsal aspect that there cannot remain the slightest doubt upon the subject. But a new specimen, from the Enniskillen Collection (no. V. fig. 5), still further demonstrates its prehensile character in the individuals that possess it ; for a number of blunt conical tubercles, without radiated bases, are clustered together upon its inferior aspect (*h*) to oppose the group of more slender hooklets already described at the base of the snout. When well preserved (as in no. I.), the surface of the spine exhibits the reticulate impressions of the vessels in a once enveloping integument [1] ; and on each side there is a marked longi- tudinal groove (fig. 5, *g*), which gradually disappears on approaching the distal extremity.

The peculiar *form* of the spine is also worthy of note, more parti- cularly as it is repeated in two other cartilaginous fishes whose remains have been found in the same geological formation ; it differs but little from that of the rostral appendage in the chimæroid *Ischyodus* [2], and is still more similar to another Liassic spine which there is some reason for suspecting may belong to the remarkable *Prognathodus* [3]. The peculiar shape, indeed, taken together with

[1] Mr. Boulenger has kindly helped me to determine that the corresponding appendage in the living *Chimæra monstrosa* is likewise covered with skin.

[2] Sir P. Egerton, " On a new Chimæroid Fish from the Lias of Lyme Regis (*Ischyodus orthorhinus, ♂*)," Quart. Journ. Geol. Soc. vol. xxvii. 1871, pp. 275– 278, pl. xiii.

[3] Sir P. Egerton, " *Prognathodus Güntheri* (Egerton), a new Genus of Fossil Fish from the Lias of Lyme Regis," Quart. Journ. Geol. Soc. vol. xxviii. 1872, pp. 233–237.

the fact of its occurrence in more than a single type, leads to an interesting speculation, suggested to me by Professor Parker. Compared with the distinct anterior intertrabecular cartilage, which forms the axis of the rostrum in such primitive fishes as the glutinous Hags (*Myxine*)[1], scarcely the slightest difference in form can be noted; and it seems not unlikely that we are here concerned with an admirable illustration of the principle, that the contours of superficial structures appended to the cranium are frequently determined, in the main, by the shape of the fundamental cartilages to which they are attached. The fossils, of course, do not permit a determination of the complete form of the intertrabecular cartilage in any of these types, or of its primitive distinctness; but the slight glimpses that can be obtained are rather favourable than otherwise to such a conclusion.

Of the skin itself in *Squaloraja*, only indefinite patches remain, and no small shagreen granules appear to have been developed in it; but the sharp lateral edge, both of the rostral and caudal regions, is strengthened by a series of minute calcified rings (fig. 1, *d*), evidently quite similar to those stiffening the boundaries of the snout in the living Pristiophoridæ.

Cranium and Mandibular and Hyoid Arches.—Nearly all the large fossils under consideration reveal facts of more or less interest in regard to the structure of the skull; nos. I., II., and IV., with Riley and Davies's specimens, present the dorsal aspect, while no. III. and the fragment shown in Davies's plate, fig. 4, afford some particulars as to the conformation of the ventral surface.

The palato-trabecular region (figs. 1, 2, *pa.tr*) extends far forwards in its present crushed condition, and from the centre is produced the long narrow intertrabecular cartilage (*i.tr*) forming the axis of the snout. From each anterior outer angle of this region there also arises a more slender forwardly directed cartilage (*pr. pa*), which gradually tapers to an incurved point, as admirably shown in the left side of no. IV. (fig. 2). This prolongation evidently served to stiffen the edge of the base of the snout, exactly as its well-developed homologue in the living *Pristiophorus*; and there can be little doubt that it represents a definite prepalatine element, such as has not hitherto been recognized in the skulls of the Selachian order. Its form is almost identical with that of the corresponding cartilage in the Myxinoids, as will be at once seen on referring to Prof. Parker's beautiful figures of *Myxine* and *Bdellostoma*[2]; in these fishes, indeed, the process serves a similar purpose, being likewise placed to strengthen the sides of the rostrum.

Immediately behind the origin of the prepalatine " horns," the lateral boundary of the palato-trabecular region gradually curves inwards for some distance, and then as slowly outwards again until it forms a well-marked antorbital prominence; but the olfactory capsules, in their fossilized state, are totally unrecognizable, though

[1] W. K. Parker, "On the Skeleton of the Marsipobranch Fishes.—Part I. The Myxinoids," Phil. Trans. 1883, pl. x. fig. 2.

[2] W. K. Parker, *loc. cit.* pl. x. figs. 1–3 and pl. xvii. figs. 1–3.

the two excavations at the base of the rostrum in the fragment shown in Davies's fig. 4 evidently testify to their normal proportions and situation. In a line with the prominence is fixed the base of the rostral spine (*r.s*), quite at the hinder extremity of the ethmoidal tract; and still more posteriorly, the chondrocranium begins to exhibit considerable lateral compression, though finally widening to a slightly broader occiput.

Extending backwards from the antorbital process, the slender postpalatine cartilage (*pt.pa*) is preserved in most specimens (especially in no. IV. fig. 2), but there is some uncertainty as to whether it formed a distinct element. It tapers slightly to its distal end, and the crushing during fossilization has usually imparted to it the deceptive appearance of connection with the hyomandibular.

No postorbital process can be observed, and the circumstances of preservation are probably accountable for the absence of any trace of a fontanelle in the cranial roof; but there is an interesting V-shaped protuberance (*a.v*) close to the hinder extremity, evidently representing a fold round the hollow into which opened the *aqueductus vestibuli* (or *ductus endolymphaticus*) of each auditory sac.

On the ventral aspect, the parachordal, or " investing mass " (fig. 3, *iv.m*), is produced posteriorly into a pair of occipital condyles (*oc.c*), as already noted by Riley; and there is a well-marked median ridge (*n*), obviously due to the remains of the primitive notochordal sheath. A median foramen (*c.f*) is also somewhat conspicuous, and, if not the result of accident during fossilization, is evidently the passage for the united internal carotid arteries proceeding to the pituitary body [1].

Of the mandibular and hyoid arches, the hyomandibular cartilage (figs. 1, 2, *hm*) is the only portion satisfactorily preserved. In its crushed condition it is seen to extend from each side of the occiput, curving outwards and forwards, and gradually tapering to the distal extremity. In shape it approximates to that of most " Batoidei," being twice as broad proximally as distally, and its apparent continuity with the cranial roof is probably due to the process of fossilization. Not a trace of the pterygo-quadrate and mandibular cartilages appears exposed to view; but the arrangement of the dental plates in the specimen no. III. (fig. 3, *t*) shows that the two rami of the jaw met at the symphysis in a comparatively acute angle, and were not placed in the same straight line, as is the case in so many living Rays.

But the most remarkable feature to be noticed in the skull of *Squaloraja* is presented in the two pairs of transversely elongated appendages, with reflected ends, arising from *beneath* the narrow part of the palato-trabecular region. These curious structures are not well shown in our fig. 1 (*ci.a*, *ci.b*), but can be studied in their entirety in the large specimens figured by Riley and Davies. The most anterior (*ci.a*) is the larger, and is completely displayed on both sides of the last-named fossil; its total length is equal to three times the width of the skull at the position where it emerges,

[1] See T. J. Parker, ' Zootomy,' 1884, p. 62, fig. 20.

and for two thirds of its extent it is directed outwards and ex-
hibits only very slight tapering ; the distal third rapidly diminishes
to a pointed extremity and is fixed at right angles to the rest in a
backward direction.   The hinder appendage (*ci.b*) measures only
two thirds the length of the first, and is about half as broad ; it
likewise has an outward and posterior trend, but (in its fossilized
state) is much more gradually arched.

The relatively great size of these appendages renders them some-
what difficult of interpretation, and it is scarcely possible to decide
whether they consist of true cartilage or are merely dermal in cha-
racter.   In position they correspond very closely with the hinder
labials of many living Selachians, and also with the supposed homo-
logous rods that form the axes of the oral barbels in Myxinoids[1].
But in the latter group these appended " feelers " never seem to
extend outwards to a length much exceeding half the breadth of the
head ; and the largest cirri with which I am acquainted in the Sel-
achians are scarcely longer than the rami of the jaws.   It seems
likely, however, that the structures in *Squaloraja* are the gigantic
representatives of the latter, which are elongated outgrowths of the
cartilages of the nasal valves[2].

There is no evidence of anterior labials in the specimens of *Squa-
loraja* already known.

Dentition.—The dentition of *Squaloraja* is very remarkable and
has not hitherto been correctly noted.   Some indications are to be
observed in specimens I. and II., but the teeth are beautifully dis-
played both in III. and IV. ; moreover, the parts in these two
instances are practically identical, showing that there were no vari-
ations according to sex, as is the case among certain living Selachians
(e. g. *Raja*).   The dentition of both jaws is preserved in no. III.
(figs. 3, 4), but only that of the right side of the mandible affords a
good view of the grinding-surface.   Each ramus bears only a single
dental plate, sharply marked off in front from its fellow of the oppo-
site side, and exhibiting towards the symphysis a gently tumid
prominence.   For the anterior two thirds of its length the plate is
of nearly uniform breadth, but in the last third the outer border
gradually trends inwards, producing a more or less pointed posterior
extremity.   And the efficiency of the grinding-surface is increased
by a series of parallel longitudinal ridges or folds of the enamel, which
are distinctly worn down towards the outer functional border.   Eleven
of these rugæ can be counted on no. III. (fig. 4), while fourteen or
fifteen are visible in no. IV ; but, except on the *under* surface of the
plate in no. II., there are no traces of any sutures between them, and
even in this specimen the evidence is somewhat obscure.   It
appears, however, that there were feebly marked longitudinal divi-
sions corresponding to the several rugæ, and that these became
accentuated at the outer edge, allowing of the shedding of the worn-
out portions as growth proceeded.

[1] W. K. Parker, *loc. cit.* pp. 385, 399, pls. x., xvii. figs. 1–3.
[2] The " Nasenflügelknorpel " of Müller ; see C. Gegenbaur, 'Das Kopfskelet
der Selachier,' pp. 97–111, pls. xvi., xvii.

Vertebral Column.—In the subject of fig. 1 the vertebral column is beautifully shown beyond the shoulder-girdle, though somewhat imperfect in front. As already described by previous writers, the vertebræ (fig. 8) are merely slender, concentrically marked rings, of the truly " tectospondylic "[1] type, and in the space just mentioned no less than 340 can be counted; in the abdominal region, sixteen of these occupy the length of a centimetre, while in the tail the proportions are so slightly different that only one more ring is comprised within the same distance. The obscure portion in front of the pectoral girdle measures one and a half centimetres in length, probably representing about 24 vertebræ; and if three centimetres are missing from the end of the tail[2], this loss will indicate an additional 48. The total number is thus found to be approximately 400, as estimated by Davies in the large specimen described in 1872.

In the more aged individuals (*e. g.*, no. II.) the vertebral rings are more robust than those of the apparently young (*e. g.*, no. III.); and it is remarkable that in no example is there any trace of the fusion of the elements in the region of the neck.

But it is not necessary to add a detailed account of the structure of the vertebræ themselves, for they have already been carefully examined and described by no less an authority than Professor Carl Hasse, of Breslau[3]. As the result of his researches in this direction, the latter anatomist concludes that in *Squaloraja* " we have to do with an ancestral form of the now living Pristidæ, a form which, in its development, appears to have advanced beyond the existing Pristiophoridæ, and also beyond the oldest Rhinobatidæ," which he has described from the upper Oolite of Bavaria.

The vertebral arches were not of sufficient consistency to leave the slightest trace in the fossil state.

Appendicular Skeleton.—In the subject of fig. 1, as already remarked, the pectoral fins are sufficiently well preserved to exhibit their complete severance from the cephalic region and their correspondence in general character to those of the living *Pristiophorus*. But the remains of the supporting girdle are much less perfect and satisfactory, and the other known specimens do not appear to throw any further light upon the subject. There can be little doubt, however, that the " girdle " was complete, as in the Rays proper, and the well-defined cartilage (*s.sc*) on the right is evidently the characteristic suprascapula. A faint trace of the posterior boundary of the transverse coracoid bar (*cor*) is also shown on the same side.

The proximal cartilages of the fin are only two in number, and well preserved on both sides of the fossil, though most completely displayed on the left. The preaxial element (*pms*) is elongated in a transverse direction, and appears of almost uniform breadth, though its exact shape is evidently destroyed by crushing; it is relatively small, having only about one quarter the size of the postaxial ele-

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[1] C. Hasse, 'Das natürliche System der Elasmobranchier,' allgemeiner Theil (1879), p. 44.

[2] The caudal region of the fossil is not completely shown in fig. 1.

[3] C. Hasse, " Einige seltene paläontologische Funde," Palæontographica, vol. xxxi. (1885) p. 4, pl. i. figs. 2, 3.

ment. The latter (*mtp*) is triangular in form, and elongated antero-posteriorly ; the foremost border abuts against the hinder edge of the preaxial cartilage, which it equals in transverse extent ; and the inner border curves gradually outwards and backwards to meet the nearly straight external boundary at a posterior apex. Judging from the analogy of living Selachians with fins of a similar type, the posterior of these cartilages may be regarded as the metapterygium ; while the anterior element may represent the coalesced pro- and mesopterygium (as in *Pristiophorus*[1]), or it may be wholly meso-pterygial, with a minute, indistinguishable propterygium at its proximal angle (as in *Heptanchus* and *Hexanchus*[2]).

Beyond the basal cartilages are arranged the cartilaginous rays of of the fin (*r*). These are somewhat obscured both in front and behind by remains of the integument, and it is uncertain whether the first attached to the preaxial element is stouter than the remainder; twenty rays, however, can still be counted on the right side, and there are traces of sixteen on the left ; the foremost thirteen are directed almost transversely or outwards, while the following have a more marked backward inclination.

The *pelvic girdle* and its appendages are rather more satisfactorily displayed than the pectoral structures just described. Anteriorly, on each side, the cartilage is prolonged into a remarkably strong prepubic process (*p.pb*), the base of which occupies one fourth of the entire breadth of the girdle ; but the forward extent of the prominence is not determinable, owing to imperfect preservation. Posteriorly, on each side, is a long slender iliac process (*il*), especially well seen on the left, and slightly directed outwards ; it is much less robust than the prepubic, and appears of almost uniform breadth throughout ; in length it equals twice the width of the transverse pubic cartilage (*pub*). Arising immediately within the point of union of the pubic and iliac regions is the basal cartilage (*b.s*) of the pelvic fin, which exhibits no sutural divisions, and (this specimen being a male) is prolonged backwards into a powerful clasper (*cl*). It curves gradually inwards throughout the whole of its rayed portion, and is of almost uniform breadth. On passing into the claspers, the cartilage becomes more calcified, and perhaps slightly broader. The inner edge is straight, but the outer edge exhibits a gentle sigmoid curve, which results in the widening of the rounded terminal extremity ; and at the end of each clasper (especially the left) a small tuft of dermal hooklets (*hk*) is preserved. The fin-rays (*r*), which appear to be completely shown on the right, are altogether twelve in number, and the length of the supporting cartilage is scarcely more than one half of that of the appended clasper. There is no distinct evidence of one or more preaxial rays attached to the girdle itself, and the foremost exhibited is no longer than the remainder.

[1] St. G. Mivart, "Fins of Elasmobranchs," Trans. Zool. Soc. vol. x. p. 453, pl. lxxviii. fig.1.

[2] C. Gegenbaur, "Schultergürtel der Wirbelthiere, und Brustflosse der Fische," Untersuch. vergl. Anat. Wirb. 1865, pl. ix. figs. 1, 2.

AFFINITIES AND SYSTEMATIC POSITION.

Proceeding, lastly, to a consideration of the systematic position of *Squaloraja*, it will be observed that the new fossils here described enable us to arrive at a much more definite conclusion than it has hitherto been possible to formulate.   Agassiz has pointed out the affinities of the genus with the Pristiophoridæ; Davies has further indicated some resemblances to the Rhinobatidæ, and been led, by his discovery of the rostral spine, to speculate at least as to its family distinctness ; while Günther[1] has likewise refrained from more than a suggestion that it is nearly allied to the first-named group.

That the animal is a true Selachian, there cannot be the slightest doubt ; nor does it require more than a superficial glance to recognize its resemblance both to the Sharks proper and the Rays.   But (as already mentioned by Davies) the possession of a prehensile rostral spine by the male distinguishes *Squaloraja* from all known members of the order, recent or fossil, and suggests affinities with the Chimæroids[2] ; while the enormous size of the barbels or cirri seems to have no parallel, at least among living forms.   The dentition, too, is evidently unique, so far as our present knowledge extends, and the marked character of the symphysis is a feature of peculiar interest.

Comparing the genus in other points with the various recognized families upon the "borderland" of the two sections of the Selachii, reference may first be made to the Rhinidæ.

Though agreeing with this group in the very slight depression of the body, it is readily distinguished by the elongation of the snout and the inferior position of the mouth ; and the anterior border of the pectoral fin is much less produced forwards, owing to the relatively smaller size of the propterygium.

To the oft-mentioned Pristiophoridæ, *Squaloraja* bears a remarkable resemblance, both in the structure of the snout and the general form of the body ; but there are no traces of teeth on either boundary of the rostrum ; and if the peculiar dental armature of the jaw may be quoted as a family character, this, too, will exclude the genus from the present group.

From the family of Pristidæ, the Liassic form is still further separated by the characters of the head and its anterior prolongation, though agreeing tolerably well in the shape of the trunk and fins.

There are also certain features that prevent its reference to the Rhinobatidæ.   The structure of the pectoral fin in this family is quite distinct from that of the fossil, the propterygial element being prolonged far towards the head, so that in some cases it is connected by skin with the cephalic region.

Its distinctness from other families is too obvious to require any special mention, and *Squaloraja* is thus excluded from all recognized divisions of the order.   It may even represent a hitherto unknown

[1] A. Günther, 'Study of Fishes' (1880), p. 335.

[2] We regard the Chimæroidei as a distinct *order*, following Professor Huxley, Proc. Zool. Soc. 1876, p. 57.

suborder, but I venture at least to suggest that the genus may be regarded as the type of a new family ; and utilizing, as far as possible, the structural features that commonly enter into the diagnoses of zoologists who study living forms, it may be provisionally defined as follows.

Order SELACHII.

Suborder TECTOSPONDYLI.

Family SQUALORAIIDÆ.

Body scarcely depressed, elongate. Head produced into a long flat rostrum, without lateral teeth. Males with a prehensile spine on the upper part of the snout. Dentition sharply divided at the symphysis. Pectoral fins with small propterygium, free.

EXPLANATION OF PLATE LV.

Fig. 1. Skeleton of *Squaloraja polyspondyla* (male), dorsal aspect. [No. I.] *a.v*, situation of auditory openings ; *b.s*, basipterygium of pelvic fin ; *ci* (*a* and *b*), cirri ; *cl*, clasper ; *cor*, coracoid ; *d*, edge of skin ; *hk*, dermal hooklets ; *hm*, hyomandibular ; *il*, iliac process ; *itr*, intertrabecular rostrum ; *mtp*, metapterygium ; *oc.c*, occipital condyle ; *p.pb*, prepubic process ; *pa.tr*, palato-trabecular region ; *pms*, preaxial basal cartilage of pectoral fin ; *pr.pa*, prepalatine process ; *pt.pa*, postpalatine (antorbital) process ; *pub*, pubic cartilage ; *r*, cartilaginous fin-rays ; *r.s*, rostral spine ; *s.sc*, suprascapula ; *t*, dentition ; *v*, vertebral column.

2. Skull of ditto (male), dorsal aspect. [No. IV.] Refs. as above.
3. Skull of ditto (young female), ventral aspect. [No. III.] *c.f*, carotid foramen (?) ; *iv.m*, investing mass ; *n*, notochordal sheath.
4. Dental plate of right mandibular ramus of ditto, twice nat. size. [No. III.]
5. Rostral spine of *Squaloraja*, sp., side view. [No. V.] *h*, hooklets ; *g*, lateral groove.
6. Rostral spine of *Squaloraja tenuispina*, dorsal view. [No. VIII.]
7. Tail of *Squaloraja polyspondyla* (young female). [No. III.]
8. Section of vertebra of ditto. [No. II.]

All the specimens are from the Lower Lias of Lyme Regis, and preserved in the British Museum. With the exception of fig. 4, the drawings are of the natural size.

3. On an apparently new Parrot of the Genus *Conurus* living in the Society's Gardens. By P. L. SCLATER, M.A., Ph.D., F.R.S., Secretary to the Society.

(Plate LVI.)

On the 29th of April last we purchased of Mr. Cross, of Liverpool, an example of a Parrot of the genus *Conurus*, which seems to be different from every other species of the genus yet described. The bird, which is still living in the Parrot-house, is at once distinguishable from its congeners by its red throat and collar, whence I propose to call it

J. Smit lith

Hanhart imp

CONURUS RUBRITORQUIS

CONURUS RUBRITORQUIS, sp. nov.   (Plate LVI.)

Green: white of throat and collar only slightly apparent; at the back of the neck bright red; eye-region naked; bill and feet whitish. Whole length 11·5 inches, wing 5·0, tail 4·7.

Hab. South America or West Indies.

Obs. About the size of *C. enops,* but distinguished by its red throat and green under wing-coverts.

4. On an undescribed *Pimelepterus* from Port Jackson.   By J. DOUGLAS OGILBY, Department of Fishes, Aust. Mus. Sydney.   (Communicated by F. DAY, C.I.E., F.Z.S.).

PIMELEPTERUS MERIDIONALIS, sp. nov.

B. vii. D. 10–11/12. A. 3/10. V. 1/5. P. 17. C. 17. L. lat. 57–59. L. tr. 10/19. Cæc. pyl. ca. 460. Vert. 11/15.

Length of head from 4·85 to 5·15, of caudal fin from 4·66 to 5·00, of pectoral fins from 7·00 to 7·20, height of body from 3·00 to 3·20 in the total length. *Eyes:* diameter from 4·00 to 4·50 in the length of the head, from 1·60 to 1·75 in that of the snout, and from 2·00 to 2·30 in the convex interorbital space. Body oblong, compressed; a transverse rounded protuberance in front of the eyes. Cleft of mouth small and transverse; upper jaw rather the longer; the maxilla reaches to below the anterior margin of the orbit. Pre-, sub-, and interopercles entire. *Teeth:* a single row of strong curved conical teeth in each jaw, the horizontal portion of which is of equal length with the vertical; behind these rows are narrow bands of similar but much smaller teeth, which probably are intended to finally replace the outer row; vomer, palatines, and tongue densely crowded with minute teeth [1]. *Fins:* dorsal spines of moderate strength, increasing in length to the seventh, which is about one half the length of the head, and much longer than the rays of the dorsal, though only equal to the first anal ray. Pectorals rounded, rather longer than the ventrals, and from two thirds to three fourths the length of the head. Third anal spine longest and strongest; caudal emarginate. *Scales* feebly ctenoid, extending in front of the eyes; much smaller on the head; 18 between the bases of the ventrals and the lateral line, and 8 between that and the base of the sixth dorsal spine; those below the lateral line larger than those above it. *Pseudobranchiæ* well developed. *Gill-rakers* 20. *Colours* dull brownish grey, with a silvery shade below; upper part of head darkest; all the fins dark. Irides a mixture of orange and silver.

[1] In connection with the dentition of *Pimelepterus,* I may mention that *Girella tricuspidata* has a small patch of palatine teeth. Dr. Günther (Cat. i. p. 427) states that "in one species there is a short series of palatine teeth," but he omits mentioning which species possesses this series.

The examples from which this species is described measure respectively 25·10, 26·10, and 28·30 inches, and were all taken in Port Jackson, where this species is locally known as the "Drummer"[1]. I have never seen a small specimen of this fish.

Breeding : only one, the largest of my specimens, showed any signs of breeding ; this was a male with the milt but little developed ; all three were taken during the month of August.

As food : not held in any estimation, and commanding no sale in the market, nevertheless it is, in my opinion, quite equal to the other herbivorous Sparoids.

Habits : in these it is a true rock-fish, dwelling in the crevices and indentations of our rocky shores, where it finds abundant food and shelter ; it is not given to roaming, and is only taken by the trammel, one end of which is attached to the shore, against which the mesh must actually lie, or else the fish would assuredly pass inside, whence it happens that this species is almost always caught within a few feet of the shore.

Note.—From Dr. Ramsay's MS. notes on Australian Fishes, I find that, so far back as 1881, he noticed these differences with regard to the dentition, but never published any communication thereon.

5. On the South-African Tortoises allied to *Testudo geometrica*. By G. A. Boulenger.

(Plates LVII. & LVIII.)

Upon the suggestion of the Rev. Mr. Fisk, of Cape Town, who has enriched the Society's Menagerie with so many interesting Reptiles, I have undertaken a reexamination of the South-African Tortoises allied to *Testudo geometrica*, and am able to distinguish as many as seven well-marked species, of which the diagnoses follow. The specimens named *T. trimeni*, after the Director of the South-African Museum, and *T. fiski*, were lately exhibited in the Society's Gardens, and were unrepresented in the Natural History Museum. That named *T. smithi*, after the author of the 'Illustrations of South-African Zoology,' is established on a specimen erroneously referred by Gray to *T. verreauxii*. The true *T. verreauxii* being still unrepresented in our collections, its diagnosis is compiled from Smith's description and figure.

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[1] It shares the name with *Girella elevata*, Macleay, and *Pachymetopon grande*, Günth. In the 'Annals and Magazine of Natural History' for November 1886, Dr. Günther described *Pimelepterus sydneyanus*, n. sp., from Port Jackson, and suggested that *Pachymetopon grande* (Cat. Austr. Fish. i. p. 106) may be *Pimelepterus fuscus*, Lacépède, and that *Pachymetopon squamosum*, Macleay and Alleyne (Proc. Linn. N. S. Wales, i. p. 275, pl. ix. f. 1), may be *Pimelepterus cinerascens*, Forsk., or *P. tahmel*, Rüppell.

J. Smit del et lith

Mintern Bros. imp.

TESTUDO TRIMENI.

TESTUDO FISKI.